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Cranial Foramina and Relationships of *Eutypomys* (Rodentia, Eutypomyidae)

JOHN H. WAHLERT¹

ABSTRACT

Derived characters of the sphenopalatine, interorbital, and dorsal palatine foramina are shared by the Eutypomyidae and Castoridae. These support the hypothesis that the two fami-

lies had common ancestry in a stem species from which no other rodent groups are descended. The two families may be included in a monophyletic superfamily, Castoroidea.

INTRODUCTION

Eutypomys is an extinct sciuromorphic rodent known in North America from strata that range in age from latest Eocene to early Miocene. The genus was named by Matthew (1905) based on the species *Eutypomys thomsoni*. "Progressive" characters of the teeth and hind feet led Matthew to ally it with the beaver family, Castoridae. He pointed out that it retains many primitive features in common with the early ischyromyoid rodents and lacks the postorbital process, a derived character of the Sciuridae. Miller and Gidley (1918) remarked on dental similarities of *Eutypomys* with the Eomyidae, an extinct group now believed to be allied to the Geomyoidea. Schaub (1958) agreed with this view and disagreed with the relationship to beavers. Stirton (1935) did not include *Eutypomys* in his study of Tertiary beavers, but he showed the genus in his phylogeny (*ibid.*, chart 2) as related to the Mylagaulidae. Wood (1937) redescribed Matthew's type specimen in detail and

gave more characters shared with castorids; he, too, found many features in common with the ischyromyoids. Wood noted the similarity of molar crown pattern to that of *Paramys* and explained it as a parallelism that possibly indicates relationship. Wilson (1949b) pointed out that the dental pattern of *Eutypomys* is more like that of sciuravids than that of paramyids. He remarked that "The presence of *Eutypomys* in the fossil record, with its mingling of sciurid and castorid features in both skull and skeleton, is perhaps an additional reason to those usually given for regarding the beavers and squirrels as related, although it must be held in mind that many of those features are primitive, retained in varying degree by the later sciuromorphs" (*ibid.*, p. 109).

Within the last 15 years, new specimens have been described and new species named: Wood and Konizeski (1965); J. R. Macdonald (1970); L. J. Macdonald (1972); Russell (1972); and Wood (1974a). Wood and Konizeski (1965) dis-

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cussed the proposed relationships of *Eutypomys*. They said that "In view of how little is known about *Eutypomys*, either as to its ancestry or as to the evolutionary trends within the genus, it is difficult to separate primitive from specialized features" (*ibid.*, p. 495). They interpreted the absence of an ectolophid on the lower cheek teeth, the major difference from the crown pattern of *Paramys* (Wood, 1937), to be a derived character. They favored castorid affinity. Wood (1974a), on the basis of new specimens of greater age than those previously known, proposed that eutypomyids and castorids are independently derived, and that eutypomyids are related to the late Eocene genus *Janimus*, which Dawson (1966) named and described as a probable microparamyine descendant. Excellent figures of the dentitions of *Eutypomys* specimens may be found in the papers cited above; the most detailed, recent discussion of crown pattern is presented by Wood (1974a).

Wahlert (1972) compared the cranial foramina of protrogomorphous and sciurumorphous rodents and found evidence to support relationship between the Eutypomyidae and Castoridae. In his detailed study of castorid dentitions, T. M. Stout (personal commun.), favored inclusion of the Eutypomyinae as a subfamily of the Castoridae. He placed the genus *Anchitheriomys* in that subfamily.

While I was curating the fossil rodents in the Frick and Cook Collections at the American Museum of Natural History, four partial skulls of *Eutypomys thomsoni* came to light. These specimens make possible a more thorough and accurate description of the cranial foramina than I could achieve in 1972. I follow the methodology of cladistic analysis set forth by Hennig (e.g., 1966), Brundin (1966), and others. Comparison of the foramina in *Eutypomys* with those in protrogomorphous and sciurumorphous rodents yields evidence for distinguishing primitive and derived characters and for testing hypotheses of relationship, based primarily on dental characters, of the genus to other rodents. It is not possible to consider every one of these hypotheses because comparative skull material for some of the extinct taxa is wanting. Further information about specific foramina may be found in Wahlert (1974). For the most part I use the names of

taxa as given in Wood's 1955 classification of the Rodentia.

I am grateful to Prof. T. Mylan Stout for sharing his unpublished information and ideas on beaver relationships, to Drs. Richard H. Tedford and Eugene S. Gaffney for useful criticism of the manuscript, and to Mrs. Katherine H. Wahlert for accommodating my irregular research schedule.

CRANIAL FORAMINA OF *EUTYPOMYS THOMSONI*

Specimens. Abbreviations of specimen completeness: c, cranium; n, snout; o, orbit; p, palate; s, entire skull; t, pterygoid region. The American Museum of Natural History: AMNH 1423 pot, Cheyenne River, Big Badlands, S.D.; AMNH 12254 type npoc, Quinn Draw, Shannon Co., S.D.; AMNH 98531 potc, Roberts Draw, Sioux Co., Nebr.; F:AM (Frick: American Mammals) 64002 npo, Cottonwood Pass, Shannon Co., S.D.; F:AM 65296 s, 1.5 miles south of Cottonwood Pass, Shannon Co., S.D.; F:AM 65297 npo, 7 miles south of South Heart, Stark Co., N.D. Carnegie Museum: CM 9839 npo, Little Badlands, Stark Co., N.D. Field Museum of Natural History: FMNH, UM 1492 np, east of Trunk Butte, Niobrara Co., Wyo. All specimens are of Orellan age.

Figure 1 illustrates most of the foramina described. It is a composite diagram of the seven American Museum of Natural History and Carnegie Museum specimens. It is not an accurate representation of any one specimen.

The ratio of length of the incisive foramina to diastemal length, measured in a direct line from the back of the incisor alveolus to the front of the alveolus of the third premolar, ranges from .26 to .30. The lateral margins of the foramina are intersected near the back by the premaxillary-maxillary suture, which runs posterolaterally away from them.

The pair of posterior palatine foramina is within the palatine bones medial to the junction of the first and second molars in five specimens and medial to the front of the second molars in two specimens; they face anteroventrally. A minute foramen medial to the back of the second molars is sometimes present either paired or asymmetrically single. The maxilla ends behind

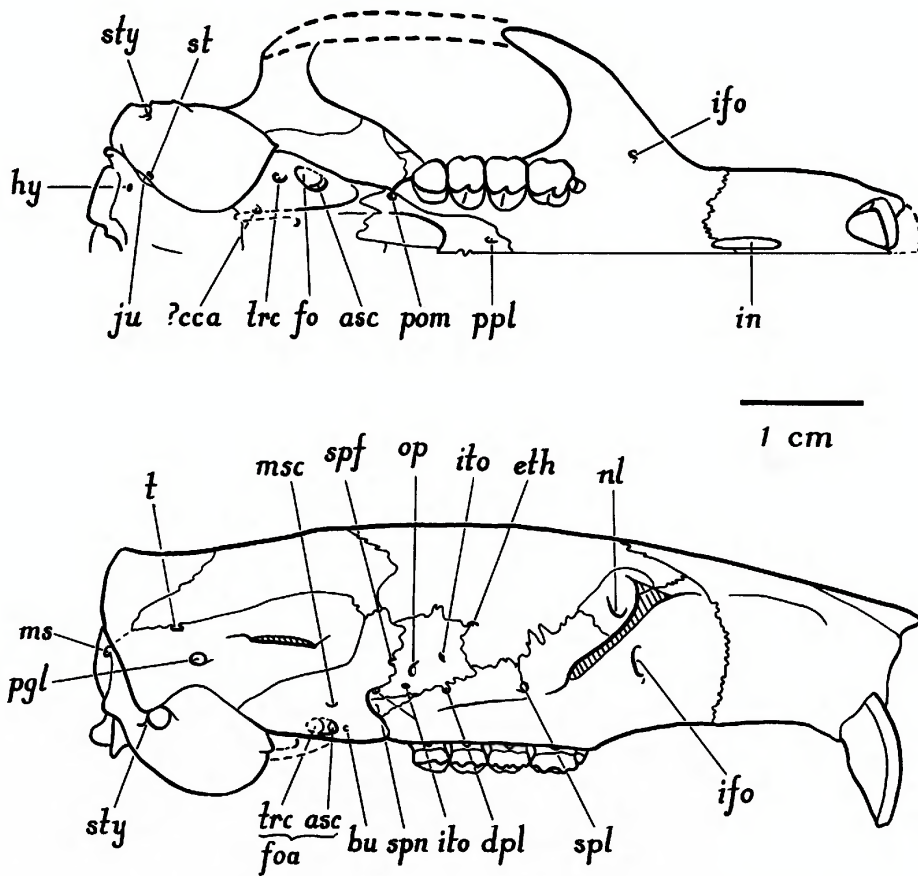


FIG. 1. Cranial foramina of *Eutypomys thomsoni* (composite of seven specimens).

Abbreviations: asc, alisphenoid canal; bu, buccinator; cca, anterior end, carotid canal; dpl, dorsal palatine; eth, ethmoid; fo, foramen ovale; foa, foramen ovale accessorius; hy, hypoglossal; ifo, infraorbital; in, incisive; ito, interorbital; ju, jugular; ms, mastoid; msc, masticatory; nl, nasolacrimal; op, optic; pgl, postglenoid; pom, posterior maxillary; ppl, posterior palatine; spf, sphenofrontal; spl, sphenopalatine; spn, sphenoidal fissure; st, stapedial; sty, stylomastoid; t, temporal; trc, transverse canal. Dashed line, probable position; hatched areas, cut through bone.

the cheek teeth in a point. Between the point and the pterygoid region a posterior maxillary foramen is enclosed; it opens dorsally in the floor of the sphenoidal fissure.

Jaw musculature was sciurormorphous; the ridge which dorsally bounds the area of origin of the deep division of the lateral masseter extends onto the premaxilla. In the type and two other specimens, the lateral margin of the infraorbital foramen is prolonged anteroventrally to form a short infraorbital canal. In lateral view, this margin is vertical, and in front view it is nearly vertical. In one specimen, F:AM 64002, the margin is

not so well developed, and there is no suggestion of a canal. The medial side of the foramen is slightly depressed into the side of the snout. A rough area behind the base of the foramen, the equivalent of a masseteric tubercle, is the area of origin of the anterior superficial division of the lateral masseter. The height of the infraorbital foramen is greater in specimens with a short infraorbital canal; it ranges from 2.3 to 3.8 mm.

The anterior alveolar foramen, seen in F:AM 64002 and CM 9839, is large and directed anteriorly into the floor of the orbit behind the infraorbital foramen. The lacrimal region is damaged

in most specimens. F:AM 64002 is the only one that retains a lacrimal bone; it surrounds the entrance to the nasolacrimal canal, which opens posterodorsal to the infraorbital foramen. The canal turns anteriorly and runs through the base of the zygoma dorsal to that foramen.

The sphenopalatine foramen is dorsal to some part of the area ranging from the front half of the first molar to the junction of the first molar and fourth premolar. It is within the maxilla, the malar and palatal parts of which meet in a vertical suture above it. The orbitosphenoid and orbital process of the palatine are substantially posterior to it. The ethmoid foramen is dorsal to the second molar. A lip from the frontal overhangs it, and the orbitosphenoid reaches it posteriorly.

The diameter of the optic foramen, which is within the orbitosphenoid, exceeds 1.0 mm. The foramen is dorsal to the posterior part of the third molar, except in one specimen, F:AM 65297, in which it is slightly posterior. Within the triangle formed by the sphenopalatine, ethmoid, and optic foramina is a pit, which deepens toward and is closest to the optic foramen. This depression was probably the site of origin of the rectus muscles of the eye. A small interorbital foramen is present in the deepest part. Another interorbital foramen faces ventrally in the orbitosphenoid bone a short distance posteroventral to the optic foramen. In one specimen, AMNH 1423, a second, laterally facing foramen occurs behind this one in a region that is poorly preserved in the other skulls. The sphenofrontal foramen opens behind the optic in the alisphenoid-orbitosphenoid suture. There is no channel in the orbitosphenoid to indicate its presence. In F:AM 65296 the cranial wall is broken away, and the cast of a blood vessel leads posteriorly from the foramen to a place in the auditory region which suggests that the vessel is the superior ramus of the stapedia artery. A branch ascends from the vessel to the postglenoid foramen.

The dorsal palatine foramen is above the junction of the second and third molars either in or just below the orbitosphenoid-maxillary suture; the palatine is not exposed this far forward in the orbit. The foramen is double in CM 9839, and the posterior aperture is at the tip of the palatine wedge. The canal from the foramen can be traced in F:AM 64002; it descends through the palatine and is a channel open into the

choanae until it plunges through the palate to emerge on the ventral side.

The sphenoidal fissure at its opening is separated from the cranial cavity by a wall of bone. The fissure is dorsal and posterior to the third molar. The alisphenoid bone is well preserved in only one specimen, AMNH 1423. The buccinator foramen, which is directed anteriorly, is very close to the foramen ovale. The masticatory foramen is above the foramen ovale and opens dorsally; there is no channel leading from it on the alisphenoid. Two minute foramina in a pit occur just ventral to it; possibly they represent small branches that split off from the masseteric nerve before it emerged from the masticatory foramen.

The lateral pterygoid flange, though broken in all specimens, preserves a distinct emargination anterolateral to the foramen ovale; this is interpreted as the front of a foramen ovale accessorius. The emargination provides a window into the alisphenoid canal, and in lateral view the transverse canal in the basisphenoid is visible. A canal leading posterolaterally from the transverse toward the front of the bulla probably housed the broad connection with the posterior facial vein. The pterygoid fossa is anteroventral to the region described. Posterior to the transverse canal, a smaller channel leads anteromedially into the basisphenoid. It may represent the course of either an internal carotid artery or a vidian artery. The middle lacerate foramen was probably covered by the bulla.

Evidence of a carotid canal is unclear because all specimens are damaged. The hypoglossal foramen, situated between the condyle and the jugular foramen, is single. The auditory region (fig. 2) is well preserved in the type, AMNH 12254, and another specimen, F:AM 65296. A conspicuous channel for the stapedia artery runs laterally across the promontorium to the fenestra vestibuli. As noted above, the superior ramus of the stapedia artery can be traced beyond this point. A canal through a laterally oriented septum of bone marks its course. The facial canal is dorsal to the ramus and passes through the septum. The descending process behind the fenestra cochleae is unusual; in ultraviolet light it fluoresces like the surrounding bone. A stapedia foramen is present anterolateral to the jugular foramen between the bulla and periotic.

The postglenoid foramen is within the squa-

mosal bone. Its major axis ranges from 2.0 to 2.5 mm. long. A temporal foramen occurs in or near the suture, dorsal to the postglenoid foramen. The presence or absence of a post-alar fissure

cannot be determined. The stylomastoid foramen is in its usual position. The mastoid foramen is high, near the top of the mastoid bone. There is no squamoso-mastoid foramen.

DISCUSSION

The cranial foramina of *Eutypomys thomsoni* are compared with those of sciurormorphs (table 1) and protrogomorphs (cf., Wahlert 1972, 1974); Olson (1940) described the foramina in castorids. I am revising the published cranial descriptions of eomyids (Wilson 1949a, and Wood 1974a) currently.

Distinguishing primitive from derived character states of the foramina is possible in most instances by out-group comparison with other rodents. Contradictions were not found. In some cases primitiveness can be verified because a character state is common to mammals in general. Stratigraphic priority has not been used as a criterion of primitiveness.

The ratio of length of the incisive foramen to diastemal length has the greatest overlap with the ranges in ischyromyids, eomyids, sciurids, and

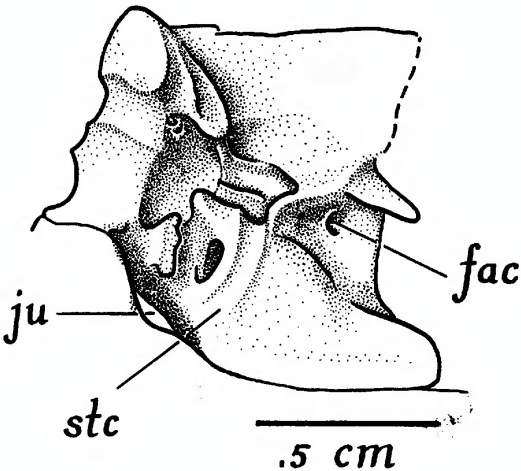


FIG. 2. Petrosal of *Eutypomys thomsoni* (AMNH 12254, type; left side, reversed).
Abbreviations: fac, facial canal; ju, jugular; stc, stapedia artery channel.

TABLE 1
Derived Characters of *Eutypomys* Shared with Sciurormorphous and Protrogomorphous Rodents

	<i>Eutypomys</i>	Castorids	Eomyids	Other Geomysoids	Sciurids	<i>Ischyromys</i> + <i>Titanotheriomys</i>	<i>Paramys</i> + <i>Sciuravus</i>
Posterior maxillary foramen enclosed	+	+	+	+	S	+	0
Sciurormorphous	+	+	+	+	+	S	0
Sphenopalatine foramen dorsal to anterior part of M ¹	+	S	+	0	0	+	0
Sphenopalatine foramen in maxilla	+	+	+	0	0	0	0
Depression for rectus muscles	+	S	0	0	S	+	0
Anterior interorbital foramen	+	S	S	+	S	+	0
Posterior interorbital foramen	+	+	0	0	0	0	0
Dorsal palatine foramen separate from sphenopalatine foramen and in maxilla or orbitosphenoid-maxillary suture	+	+	0	0	0	0	0

Symbols: +, all specimens; 0, none; S, some.

castorids (except the largest extinct genera). It is below the range in *Paramys*, *Reithroparamys*, *Sciuravus*, and *Prosciurus*. It overlaps the low end of the range in cylindrodontids, and aplodontoids, the upper end of the range in heteromyids, and is entirely above the range in *Ischyrotomus*, *Manitsha*, and geomyids.

The posterior palatine foramina are wholly within the palatine bones. This condition is regarded as primitive because it occurs in protrogomorphous rodents except the derived groups Manitshinae, Ischyromyidae, and Cylindrodontidae in which the foramina are in the maxillary-palatine suture. Only *Agnotocastor* among beavers, some fossil forms among sciurids, and eomyids among geomyoids have the foramen in the palatine. The position of the foramina relative to the cheek teeth is common among protrogomorphous and sciuriform rodents. Enclosure of a foramen for the descending palatine vein by the maxillary point is a derived condition. Other rodents that have this foramen are ischyromyids, *Pseudocylindrodon*, aplodontoids, castorids, geomyoids, and most sciurids.

A long infraorbital canal is common in mammals but exceptional in rodents. It occurs only in groups with sciuriform musculature and is a derived character. Its rudimentary development in *Eutypomys* is like that seen in certain living sciurids, e.g., *Tamias*.

The sphenopalatine foramen is far forward relative to the cheek teeth. The position is duplicated only in ischyromyids, eomyids, and in some castorids. Its situation within the maxilla is seen only in castorids and eomyids. The ethmoid foramen is in the orbitosphenoid-frontal suture, a probable primitive character since this position is common in rodents and other mammals. In prosciurids, aplodontids, and sciurids the foramen is wholly within the frontal.

The depression for attachment of the rectus muscles of the eye is unusual. A similar structure is found in ischyromyids, some prosciurids, some castorids, some sciurids, and in *Aplodontia*. The anterior interorbital foramen is present in ischyromyids, geomyids, and some members of the other three groups with the addition of some aplodontids and eomyids. The posterior interorbital foramen ventral and posterior to the optic foramen is a distinctive, derived castorid feature.

The situation of the dorsal palatine foramen separate from the sphenopalatine foramen and in the orbitosphenoid-maxillary suture or maxilla is another derived character shared with castorids.

Most of the remaining foramina of the orbit, pterygoid region, and cranium are present in their primitive states. The foramen in the posteromedial part of the pterygoid region behind the transverse canal may be homologous to a similar foramen in *Reithroparamys* and *Castor* and to an aperture interpreted as a meningeal foramen in ischyromyids (Wahlert, 1974, p. 391 and fig. 9). The presence of an internal carotid artery as in *Castor* (Guthrie, 1963, fig. 4) cannot be determined. The stapedial artery, a primitive character in rodents, is known among castorids only in *Agnotocastor*.

CONCLUSIONS

Relationships are based on the presence and number of shared derived characters. Shared primitive characters indicate only that forms belong to some larger taxon to which these characters are unique. Parallelism is not invoked as explanation unless it can be demonstrated that two similar characters are not members of the same transformation series and thus are not strictly homologous.

Eutypomys shares the greatest number of derived characters with the castorids: posterior maxillary foramen enclosed; infraorbital foramen modified by sciuriformity; sphenopalatine foramen entirely surrounded by maxilla; dorsal palatine foramen separated from sphenopalatine foramen and situated in orbitosphenoid-maxillary suture or maxilla; interorbital foramen present posterior to optic foramen. The last two characters are shared only with castorids. The castorids themselves form a monophyletic group possessing a distinctive dental pattern. That *Eutypomys* and the castorids share common ancestry and are each other's closest relative is a supportable hypothesis. A cladogram, figure 3, illustrates this hypothesis of relationship within the Castoroidea. Inclusion of the Eutypomyidae and Castoridae in the superfamily Castoroidea is the best procedure in a classification to indicate this relationship. Cranial material of *Janimus* is unknown; the genus may be a eutypomyid.

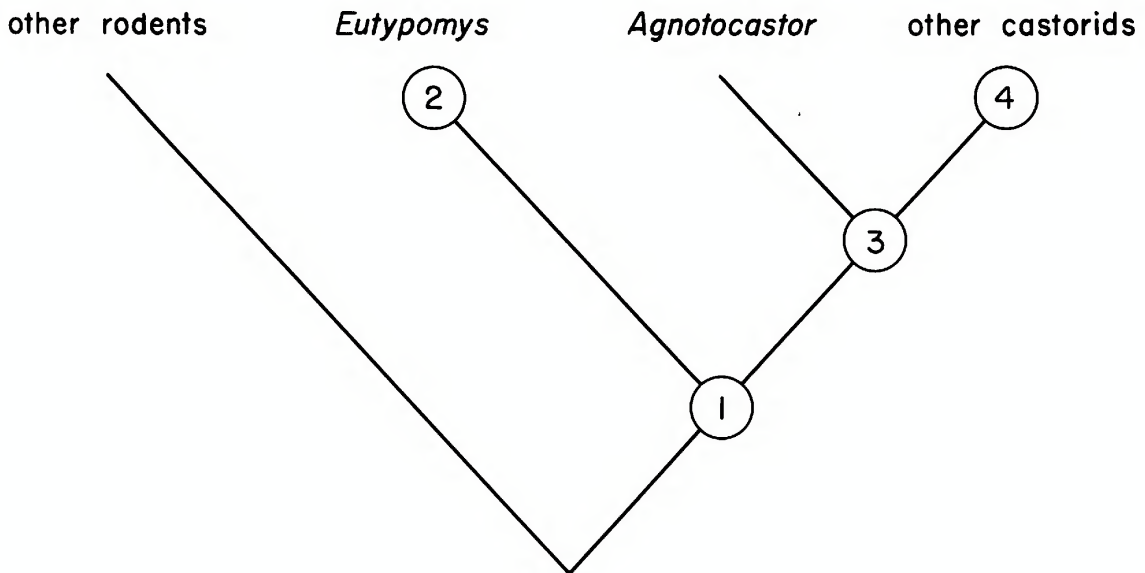


FIG. 3. Cladogram of proposed relationships within the Castoroidea. Shared derived characters: 1. Dorsal palatine foramen separated from sphenopalatine foramen and situated in orbitosphenoid-maxillary suture or maxilla; interorbital foramen present posterior to optic foramen; 2. Eutypomyid tooth crown pattern; 3. Castorid tooth crown pattern; 4. Posterior palatine foramen in maxillary-palatine suture; stapedial artery lacking.

Sciuromorphy and a long infraorbital canal have developed independently in different rodent groups. The ischyromyid genera are nearly identical except that some forms show evidence of anterior expansion of the deep lateral masseter. The same trend can be seen in sciurids, a monophyletic group based on other characters of the cranium and dentition. Wood (1974b, p. 50) stated that "the fact that similar results develop independently may be considered indicative of a common genome, producing identical phenotypic results by similar genetic methods." The fact of parallelism, therefore, does not falsify the possibility of relationship between the groups of sciuromorphic rodents.

A few derived characters are shared by *Eutypomys* and ischyromyids: posterior maxillary foramen enclosed; sphenopalatine foramen situated far forward; depression for rectus muscles present and containing interorbital foramen. Derived characters are also shared by *Eutypomys* and eomyids: posterior maxillary foramen enclosed; infraorbital foramen modified by sciuromorphy; sphenopalatine foramen situated far forward and entirely surrounded by maxilla. None

of these characters is shared only with ischyromyids or eomyids. It is interesting to note that Cope (1873) originally used one genus, *Gymnoptychus*, for both an ischyromyid and eomyids. In 1874 (p. 477) he listed the species *Gymnoptychus chrysodon* as a synonym of *Ischyromys typus*. He stated (1883, p. 50) that the dentition of *Gymnoptychus*, now *Adi-daumo*, is much like that of *Ischyromys*. As noted above, both Miller and Gidley, and Schaub found dental similarities between *Eutypomys* and the eomyids. Redescription of the cranial foramina of eomyids, which may shed new light on their relationships to other rodents, is in progress.

How *Eutypomys* is related to the various Eocene rodents cannot be determined on the basis of currently available cranial material. A close relationship to mylagaulids is not supported by shared derived characters.

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